

Direct Measurement of CO₂ Production During Flight in Small Birds¹

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(Text-figure 1)

CO₂ production during flight and rest was measured in 16 individual small birds belonging to 13 species. The birds flew back and forth in a plastic tube inflated by air pressure. The average non-flying CO₂ production was 5.4 ml/gm hr while the average flying rate was ten times the non-flying rate.

INTRODUCTION

OCEANOGRAPHERS frequently see small birds miles at sea, birds which often land aboard ship to rest. This occurs in good weather as well as in bad and one may wonder why the birds are so far from land and how much effort it requires for them to fly so far over the water.

Measurements of the energetic cost of flight in birds have been limited due to the difficulty of getting most birds to fly in a suitably confined space in which to measure metabolism. The flight, or more accurately the hovering, of hummingbirds makes them a suitable subject for such measurements (Pearson, 1950; Lasiewski, 1963). Tucker (1966) has succeeded in training budgerygahs to fly at one spot in a wind tunnel and has measured their oxygen consumption at a variety of flight speeds. Other estimates of bird flight metabolism have been made by LeFebvre (1964) and Nisbet *et al.* (1963).

I have measured the CO₂ production during flight of 16 individual birds of 13 species by getting them to fly back and forth in a plastic tube and measuring their production of carbon dioxide with an infrared gas analyzer. These flights were all short in distance and time and

may resemble flights made to escape predators more than the sustained flights typical of migration. (Throughout this paper, flight refers to flapping flight and soaring is not considered.)

Ten of the birds were from the collection at the Bronx Zoo and the measurements were made at the zoo: Baltimore oriole, *Icterus galbula*; black-capped sibia, *Heterophasis capistrata bayleyi*; blue grosbeak, *Guiraca caerulea*; blue jay, *Cyanocitta cristata*; northern scaly dove, *Scardafella squamata ridgwayi*; orange-backed silver-beaked tanager, *Ramphocelus flammigerus*; orange weaver, *Euplectes orix franciscanus*; redwing, *Agelaius phoeniceus*; superb glossy starling, *Spreo superbus*; white-throated sparrow, *Zonotrichia albicollis*. I thought that birds used to being caged and handled would be better subjects than wild birds. Later, further measurements were made on six more birds caught in mist nets in my yard in North Falmouth, Massachusetts: blue jay, *Cyanocitta cristata*; field sparrow, *Spizella pusilla*; house sparrow, *Passer domesticus*; white-throated sparrow, *Zonotrichia albicollis*; yellow-shafted flicker, *Colaptes auratus*. The wild birds were no more difficult to handle than the zoo specimens, and in two cases where the same species was used at the zoo and at North Falmouth, the wild bird's flight metabolism was lower.

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birds. I wish to thank the staff of the Bird Department at the zoo for their help in handling the birds.

METHODS OF STUDY

The flight chamber was a polyethylene tube with walls 5 mils thick and perches at each end. A single 60 watt bulb was located just outside the tube next to the perch. The tubes were inflated and kept rigid by air pressure from a blower that blew air in one end and out through a similar opening at the opposite end. At the zoo the tubing was 60 cm in diameter when inflated. The North Falmouth tube was 1 m in diameter. In North Falmouth outside air drawn from a stovepipe opening on the roof of my barn was used directly and had a suitably constant $p\text{CO}_2$ when the wind was blowing. In the Bronx the $p\text{CO}_2$ varied so much that an initial air mixing chamber of 15 m³ volume, made also of 5 mil thick polyethylene, was used to even out the variations in air composition. Air was drawn into the mixing chamber from outdoors, mixed with a fan, and blown into the flight chamber with a squirrel cage blower. The experiments at the zoo were done in May in the basement of the monkey house, where the flight tube could be no longer than 11 m. The North Falmouth experiments were done in October with a flight tube 17 m long. In both cases the experiments were done during daylight, but with the room containing the tube darkened so that most of the light came from the bulb near the perch. Air temperature in the tube was between 15° and 19°C during both sets of experiments.

At the beginning of the measurement, the bird was introduced into the tube and allowed to settle down until a steady production of CO_2 was achieved. Then the light by the bird was switched off and the light at the opposite end of the tube switched on. At the same moment the outside of the tube next to the perch was tapped and the bird flew to the opposite end of the tube. The actual time of flying was measured with a stopwatch. The opposite perch was then lighted and this was repeated until the bird had flown for from 15 to 245 seconds. The bird was then allowed to rest at one end of the tube until the $p\text{CO}_2$ returned to its preflight level and the experiment repeated. After from one to eight series of flights, the bird was removed and the background $p\text{CO}_2$ variations checked. Average flight speed was calculated from the distance between the perches at the two ends of the tube and the total flying time recorded on the stopwatch. The few seconds the birds spent on the perches was not included in the total; time spent hovering was.

The zoo birds were fed and cared for in the usual manner by their keepers. The wild birds were removed from the net, placed in a cage with food and water, and left in a quiet room for from one to several hours before an experiment. They were released after being weighed at the end of the experiment.

The $p\text{CO}_2$ was measured with a Beckman infrared gas analyzer with air from the inlet to the flight tube pumped through the reference cell, and air from the outlet pumped through the measurement cell. The outlet of the flight tube was led through a 50 cm long piece of 8 cm diameter tubing from the center of which the outlet sample was taken. This avoided difficulties arising from small changes in blower speed that could otherwise have drawn room air into the flight tube. Both streams of air were dried by passing through columns of silica gel before entering the analyzer. A solenoid-operated valve disconnected the sample gas from the measurement cell and substituted reference gas for one minute every four minutes to provide a reference level. This was turned off during the period when the flight record was taken so as not to interfere with the measurement of the area under the curve. Flight metabolism is taken as the CO_2 production, shown by the upward deflection of the curve after a flight (Text-fig. 1), divided by the flying time, plus the resting rate of CO_2 production. It required about nine minutes for all the CO_2 produced at the inlet end to be flushed completely out of the flight tube. This long time-constant made it impossible to distinguish between CO_2 produced by a bird during flight and that produced immediately afterward during repayment of any oxygen debt incurred during flight. Calibrations were made by flowing CO_2 gas into the flight tube at a measured rate of 10, 20, or 40 ml/min for from 2 to 4 minutes and measuring the area under the deflection of the $p\text{CO}_2$ curve produced. If the gas was injected near the outlet end, a large deflection for a short period was produced. This deflection had an area within 1% of that under the longer but lower deflection produced by injecting the gas at the inlet end of the tube. After each day's experiments two calibrations were done which always agreed to within 2%. Because of variations in background CO_2 level during the experiments, I consider the measurements of bird CO_2 production to be accurate between 5 and 10%. [The $p\text{CO}_2$ of the air entering the flight tube in the zoo was close to 375 ppm which the flying birds occasionally raised to as high as 410 ppm occasionally, though usually the increase was only to about 385 ppm.] The $p\text{CO}_2$ of the North Falmouth air varied

between 320 and 340, and the increase produced by the birds was from 5 to 20 ppm.

RESULTS

The results of the experiments are listed in Table I and a tracing of one of the actual recordings is shown in Text-figure 1.

Not all of the birds tried would fly in the tube. The scaly dove, the only Columbidae used, walked along the tube at the beginning of the experiment. It would fly only after I had chased it up and down the tube several times, not allowing it to settle for long. A saw whet owl also preferred to walk and I never succeeded in getting it to fly down the tube, although the attempts were made during the evening when the bird seemed awake and active.

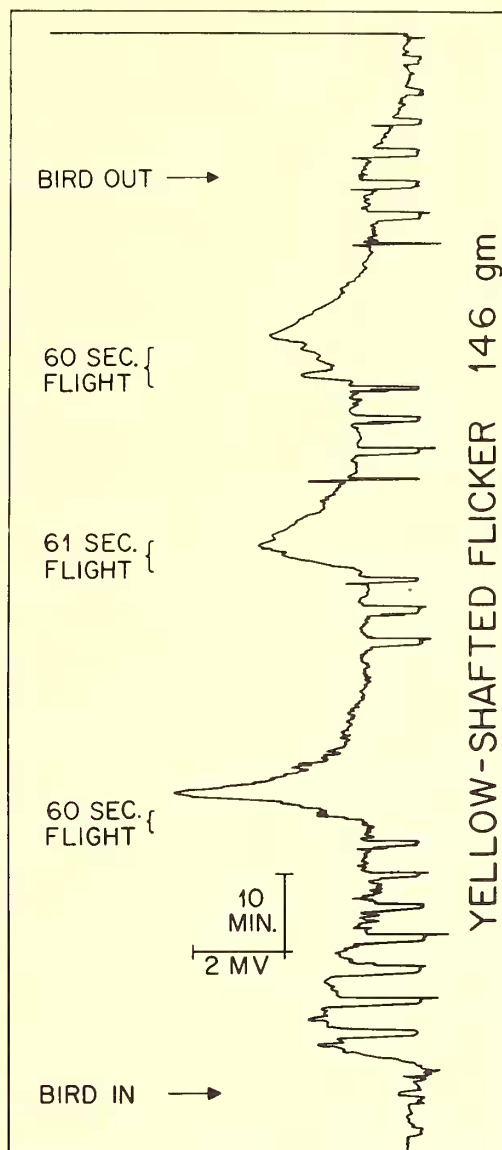
The other birds all flew after the first few times, when they would land part way along and have to be startled up again. Only those series in which the birds flew the complete length of the tube are included in the results. In most cases the birds first flew in a near-stall with tail down, fluttering near the top of the tube. Once they had learned of the perch at the opposite end, their flight became progressively more direct. Ultimately they generally flew directly down the tube; periods of wingbeat alternated with periods of gliding with folded wings, much as the birds fly when free in nature. The birds usually settled on the perch before I could start them on the return flight. The flight speeds were about one-half those considered typical for such birds. The scaly dove, Baltimore oriole, orange-backed silver-beaked tanager, and white-throated sparrow from the zoo never did achieve natural-looking, forward flight in the tube, but instead fluttered in a semi-stalled position with the tail down during their best flights. These birds showed the highest CO_2 production due to flight of all the measurements.

CO_2 Production

Some of the CO_2 production attributed to flight could have been produced by hyperventilation due to overheating, which can produce alkylsis in the blood. If this were significant it would have shown as a reduced CO_2 output during recovery from the alkylsis, which was not apparent.

In some cases, *e.g.*, the flicker, the improvement in successive flights can be seen both in the reduced CO_2 production as a result of flight and in the increased speed. In other cases, such as the black-capped sibia, the flight speed increased but the CO_2 production showed no regular change.

The birds had a total CO_2 production during



TEXT-FIG. 1. Tracing of record of carbon dioxide production of yellow-shafted flicker in polyethylene flight tube. Two millivolts equals about 15 ppm CO_2 . The downward deflections show the pCO_2 in the input air.

their most economic flights of between 40 and 77 ml CO_2 /gm hr (Table II).

DISCUSSION

Table II lists the birds' CO_2 production when not flying and for their most economic flight. The average non-flying rate of CO_2 production for all the birds was 5.4 ml CO_2 /gm hr. This corresponds to about 32 cal/gm hr, assuming

TABLE I
METABOLISM OF BIRDS DURING FLIGHTS IN PLASTIC TUBE.

Flight CO₂ is that produced as a result of flying divided by flight duration, plus resting rate of CO₂ production. More than one rest metabolism was calculated if rate changed or experiment was interrupted. (W) are wild birds, (Z) are zoo birds.

<i>Species</i>	<i>Weight gm</i>	<i>Duration of flights sec</i>	<i>Speed m/sec</i>	<i>CO₂ produced during flight ml/gm hr</i>	<i>Resting CO₂ production ml/gm hr</i>
White-throated Sparrow (Z)	32.0	31	4.3	77	7.2
		61	84
		91	3.6	86
Northern Scaly Dove (Z)	51.4	15	119	8.0
Redwing (Z)	69.3	34	4.0	81	5.2
		38	4.0	80	6.9
		60	4.0	75
		60	4.4	60
		62	5.3	63
Blue Grosbeak (Z)	21.6	67	4.3	56
		84	53	6.4
		65	53	6.4
		64	3.8	59
		79	70
		55	53
		45	4.4	51
		71	4.7	48	3.2
Orange-backed Silver-beaked Tanager (Z)	44.6	68	5.0	56
		37	86	6.4
		35	3.2	71
		48	3.7	79
Northern Scaly Dove (Z)	50.9	50	3.3	79
		46	2.2	80	2.8
		49	68
		38	2.9	63	4.7
Superb Glossy Starling (Z)	54.4	34	3.2	71
		65	3.0	71	5.5
		111	3.0	47
		85	2.6	43	5.1
		42	63
		64	48	4.7
Black-capped Sibia (Z)	38.1	67	3.6	41
		59	3.7	68	5.4
		67	4.9	68
		24	4.6	55
		32	4.8	46
		60	5.5	76
		36	6.1	63
		29	6.1	87	3.6
Orange Weaver (Z)	19.3	40	5.5	65
		60	64	11.0
		66	79
		56	74
Baltimore Oriole (Z)	38.0	72	3.0	52	7.1
		19	80	3.6
		81	2.7	63
		68	3.3	67
		33	3.4	69

Species	Weight gm	Duration of flights sec	Speed m/sec	CO ₂ produced during flight ml/gm hr	Resting CO ₂ production ml/gm hr
Blue Jay (Z)	84.0	46	63
		32	60	4.2
		17	58
		15	65	3.6
		33	69
		61	62
Blue Jay (W)	94.2	82	3.9	42	2.8
		70	4.4	51
		56	4.3	43
Yellow-shafted Flicker (W)	146.5	60	3.7	65	3.6
		61	3.9	48
		60	4.1	41
House Sparrow (W)	28.0	100	51	7.9
		100	3.4	42
White-throated Sparrow (W)	24.0	95	51	3.7
		170	2.0	51
House Sparrow (W)	30.5	110	3.3	62	8.7
		125	3.5	66
		205	3.2	59
Field Sparrow (W)	21.0	245	1.4	50

a ratio of CO₂ production to O₂ consumed of 0.8. The birds were at an average temperature of 17°. With a thermal conductance of 0.14 ml O₂/gm hr °C (Lasiewski, 1963), average non-flying metabolism would have been 22 cal/gm hr in the birds' thermoneutral zone. Since the birds were not fasting, the thermoneutral rate must be again reduced by about 1/3 (Brody, 1945). This calculation gives an adjusted non-flying metabolism of 15 cal/gm hr; this may be compared with a standard metabolic rate of 12 cal/gm hr for 50 gm passerines resting in a postabsorptive state at thermoneutrality based on data from the literature summarized by Lasiewski & Dawson (1967). The fact that the rate calculated for my birds is 1.25 times higher reflects the fact that the birds were not always completely still when they were not flying. It might also indicate that they were excited. The higher rate is perhaps closer to what Odum *et al.* (1961) call existence metabolism defined as maintenance metabolism of caged birds. Since their CO₂ production was elevated, it seems reasonable to compare the birds in terms of their most economic flights, those in which the CO₂ production rate was least.

Omitting the data for the first four birds listed in Table II, the four birds that flew poorly throughout the experiments, the average CO₂ production during flight was 49 ml CO₂/gm hr, or about 294 cal/gm hr. This is about 50% larger than the values obtained by direct measurement of oxygen consumption in flying birds; an average corresponding to about 192 cal/gm

hr for budgerigahs (Tucker, 1966), and a value of 202 cal/gm hr for a hovering Costa's Hummingbird (Lasiewski, 1963).

My values of flight metabolism are four times as large as the values calculated from experiments with isotopically labeled water for pigeons (LeFebvre, 1964), which were about seven times as heavy as the average weight of the birds I used (50 gm). My value of 294 cal/gm hr is nearly six times as large as the estimated flight metabolism for the Blackpoll Warbler of 52 cal/gm hr. The latter value was calculated from weight loss of birds migrating between Massachusetts and Bermuda (Nisbet *et al.*, 1963).

The birds in my flight tube (omitting the first four which flew poorly) used energy on the average at ten times their non-flying rate when they were making their most economic flights. Assuming that flight metabolism was unaffected by the temperatures in these experiments, the ratio would have been 13 in the birds thermoneutral zone.

Brody (1945, p. 913) found that at maximum oxygen consumption rate for a horse or man, the rate of energy use was about 15 times the resting rate, or 21 times the basal rate. Brody's resting rate is the basal rate plus the specific dynamic action of the diet, i.e., the resting rate of a non-fasting animal. He found that animals can work harder than this, as much as 100 times their resting rate, but only by assuming an oxygen debt. In the absence of other data we might

TABLE II

METABOLIC CO₂ PRODUCED DURING MOST ECONOMIC FLIGHT COMPARED TO RESTING CO₂ PRODUCTION.
(W) are wild birds, (Z) are zoo birds.

Species	Resting CO ₂ production ml/gm hr	CO ₂ produced during flight ml/gm hr	Ratio flight to resting
White-throated Sparrow (Z)	7.2	77	11
Orange-backed Silver- beaked Tanager (Z)	6.4	71	11
Baltimore Oriole (Z)	3.6	63	17
Northern Scaly Dove (Z)	5.5	63	13
Blue Jay (Z)	3.6	58	16
Redwing (Z)	6.9	56	8
Orange Weaver (Z)	7.1	52	7
Blue Grosbeak (Z)	6.4	51	8
Black-capped Sibia (Z)	3.6	45	12
Superb Glossy Starling (Z)	5.1	40	8
Field Sparrow (W)	50
House Sparrow (W)	8.7	59	7
White-throated Sparrow (W)	3.7	51	14
Blue Jay (W)	2.8	42	15
Yellow-shafted Flicker (W)	3.6	41	11
House Sparrow (W)	7.9	42	5
AVERAGE	5.4	49	10

suppose that birds have about the same limit and can do sustained work at no more than about 15 times their resting metabolic rate. Apparently on the average my birds were working just about as hard as they could. Calculations for some of the poorer flights gave ratios of flight to non-flight as high as 27 for one of the near-stalled flights of the Scaly Dove. I believe these poorer flights were associated with oxygen debts, i.e., the measured CO₂ was produced over a longer period than that spent flying.

It is conceivable but it is not probable that migrating birds are working at their maximum rate. Passerine birds migrate across the Gulf of Mexico without stopping and are even thought to fly directly from New England to South America without intermediate stops. Very few of the birds collected at the beginning of migration have enough fat to cross even the Gulf of Mexico if they expend energy at the rates we have measured in any of the direct gas measurement experiments.

Odum *et al.* (1961) estimated the flight range of birds on the basis of an existence metabolism about twice that of my birds and a flight metabolism twice their existence rate, or about half of the rate measured in my experiments. Nisbet *et al.* (1963), on the basis of their weight loss measurements, theoretical considerations, and a review of the literature, suggested that flight metabolism in migrating small birds is probably about twice resting metabolism at 10°C.

A ratio of flight to existence metabolism of 8

was found by Le Febvre (1964) for pigeons, and a ratio between flight and standard metabolism of 7 for hummingbirds (Pearson, 1950; Lasiewski, 1963). Ratios of flying to non-flying O₂ consumption between 5 and 6 for budytygahs can be calculated from Tucker (1966). The ratios for pigeons and budgerygahs would be larger if standard rather than existence metabolism were used for the denominator. These are all larger than the theoretical values mentioned above but smaller than the average found here, although I found several ratios of 7 and 8 and one ratio, for a House Sparrow, as low as 5 (Table II). I can see no particular reason to suppose that there should be a constant ratio between resting and flight metabolism in birds with different weights and aerodynamic properties, so perhaps some of the differences in these ratios may be real. There is a suggestion in Table II that the ratio varied less between measurements on two different individuals of one species than it did between species.

Hartman (1961) gives values for the portion of body weight made up by the flight muscles which permit a calculation of the metabolic activity of these muscles. The assumption is made that all of the energy used during flight above that used at rest is due to the activity of these muscles (Table III). The values ranged from 2.3 to 4.6 ml CO₂/gm min for the most efficient flights, corresponding to 2.9 to 5.7 ml O₂/gm min with an RQ of 0.8. These numbers are above the 2.7 ml O₂/gm min calculated by

TABLE III
METABOLIC ACTIVITY OF FLIGHT MUSCLES CALCULATED FROM CO₂ PRODUCTION
DUE TO FLIGHT AND ESTIMATED WEIGHT OF FLIGHT MUSCLE.

(W) are wild birds, (Z) are zoo birds.

Flight muscle weights are estimated from Hartman (1961).

Species	Weight gms	Estimated weight of flight muscle gms	Flight CO ₂ range ml/gm hr	Muscle metab- olism range ml/gm min
House Sparrow (W)	28	7	30-43	2.0-2.9
Superb Glossy Starling (Z)	54	13	35-66	2.4-4.6
Yellow-shafted Flicker (W)	147	37	147-242	2.5-4.0
Orange Weaver (Z)	19	5	45-68	2.8-4.3
Blue Jay (W)	94	21	39-48	2.9-3.6
Northern Scaly Dove (Z)	51	17	58-111	2.9-5.5
White-throated Sparrow (W)	24	6	47	3.1
House Sparrow (W)	31	8	50-57	3.2/3.7
Blue Grosbeak (Z)	22	5	45-64	3.3-4.7
Black-capped Sibia (Z)	38	8	41-83	3.3-6.6
Field Sparrow (W)	21	5	50	3.5
Redwing (Z)	69	15	49-76	3.7-5.8
Baltimore Oriole (Z)	38	9	59-76	4.1-5.3
Blue Jay (Z)	84	18	54-65	4.2-5.1
Orange-backed Silver- beaked Tanager (Z)	42	10	65-80	4.6-5.6
White-throated Sparrow (Z)	32	8	70-79	4.7-5.3

Tucker (1966) for budgeryahs and comparable to the range of 1.4 to 7.3 ml O₂/gm min reported for insect flight muscle (Weis-Fogh, 1964) and said to be the most active animal tissues known.

The flight tube experiments gave results which are about 50% higher than those obtained by measurement of oxygen consumption by flying birds but are nearly six times as large as the estimates based upon fat concentration and loss of weight during migration. With the short flight durations and paths I used, the effects of hovering at landing and takeoff are emphasized. A longer or toroidal tube might permit the birds to achieve better economy. The method used for this work is convenient in that a large number of experiments can be done on a variety of species with a minimum of time spent training the birds.

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